On the Mouth-parts of the Shore Crab.

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(Plates 10, 11.)

[Read 6th April, 1922.]

I.

The organs which stand about the mouth of a Decapod Crustacean make up a complex as intricate as any that is to be found in the Animal kingdom. They are also extremely important to their possessor, for without them the animal can neither feed nor breathe, and to one of them falls, at least in many cases, the duty of keeping clean the indispensable organs of special sense. Yet they are at present but little understood.

In a study upon the Common Prawn, published in 1917 (5), I endeavoured to solve the problem which the morphology of these organs presents, and made a beginning with the investigation of their working. This paper contains an account of some observations upon *Carcinus mœnas*, a species at the other end of the decapod series.

The term "mouth-parts" denotes, in the Crab, a number of organs which stand upon the under side of the body, in the region which is bounded behind by the anterior edge of the mass of fused postoral sterna, at the sides by the edge of the inturned carapace where this encloses the exhalent passage of the gill-chamber, and in front by the fused antennal and mandibular sterna (epistome). The sterna of the maxillulary to second maxillipedal segments inclusive are more intimately united with one another than those of the legs; and they form a mass, roughly triangular with the apex forwards, that stands out steeply from an area, in front of and beside it, which is covered by a thin cuticle supported upon the pieces of the endophragmal skeleton. It is upon this area that the mouth-parts are inserted. They are: the six pairs of limbs from the mandibles to the third maxillipeds inclusive, the upper lip or labrum, the lower lip or metastoma, and the fleshy opening of the mouth itself. I propose to describe in succession each of these parts and its movements, and then to discuss the functions of the complex as a whole.

II.

1. *The Third Maxilliped* is built upon the plan of the legs. This statement, by a phenomenon often seen in serially homologous structures, is true even of features—such as the fusion of the basis and ischium and the nature of the articulation of the joints—which cannot be supposed to have existed in the schizopod ancestor whose thoracic limbs were not differentiated from one

another. The limb is a broad structure, flattened in that direction which is morphologically antero-posterior, and widened from side to side. In what may be called the *normal position* it is turned forwards till its wide plane passes the horizontal and slopes a little upward in front. In this position it meets its fellow on the middle line, and the two form an operculum which almost wholly encloses the mouth-field, abutting behind on the sterna, at the sides upon the edge of the carapace, and in front upon the epistome save in the middle, where a gap is left through which the gill-stream can flow even when the operculum is most tightly closed. Each third maxilliped *articulates* ventrally with the hinder angle of its sternum, and dorsally (anteriorly) with the epimerite of its segment.

The *coxa* is of oval transverse section. Its proximal rim bears on the under side the knob which makes articulation with the sternum, where it is received by a saddle-shaped hollow between two processes. Adjoining this is a facet on the median surface of the joint, which works against the external (antero-lateral) face of the sternum. On the dorsal side the rim bears a socket which articulates with a correspondingly shaped process of the epimerite. On the outer side the coxa has a backward-curving flange, to which, by a flexible suture, is hinged the *epipodite*. This organ has a stout base, which bears on the dorsal side the small podobranch, and a long, blade-like process which, diving under the edge of the branchiostegite, enters the gill-chamber and passes between the posterior arthrobranch of its own limb and the anterior arthrobranch of the cheliped, to lie between the gills and the side of the body. The whole organ, and the flange upon which it is borne, is spirally twisted, so that, starting in the horizontal plane in which the main part of the limb lies below the mouth, it ends in a vertical plane against the flank. The flange and the base of the epipodite stand in that gap, between the anterior face of the coxa of the cheliped and the branchiostegite, which is the anterior inhalent opening of the gill-chamber; and their twisted shape bears such a relation to the opening that when the maxillipeds are in the normal position they lie across it and almost but not quite close it, but when the maxillipeds are divaricated, the epipodites lie in the midst of the opening, with their flat sides parallel to the stream, to which they offer little opposition. The part of the opening which is covered when the maxillipeds are approximated is the anterior. The extent to which the hinder part remains open varies with the position of the cheliped.

The *basis and ischium* are fused, though traces of their junction usually remain in the form of a groove. By this it is shown that the basis is a small region which in width makes the transition from the stout coxa to the flat ischium, and in position fills a triangular gap between them, due to the fact that the ischium is displaced to the median side of the coxa. The free (median) edge of the basis abuts upon the edge of the sternum, and continues the contact made by the facet upon the coxa. On the outer side the basis bears the *exopodite.* The stem of this is a long, narrow, flattened structure, directed forwards between the endopodite and the branchiostegite, and bearing at its end a flagellum which is directed inwards above the merus towards the middle line. The flagellum consists of a basal joint, and a many-jointed lash, curved with the concave side forwards. The exopodite stands at the junction of basi-ischium and coxa, and besides being articulated to the former is attached by membrane to the latter.

The ischium is an oblong, roughly rectangular, and very flat joint, which makes nearly half the total surface of the limb. It is succeeded by the *merus,* a flat, subquadrate structure, stouter than the ischium and tilted a little outwards upon the latter. Owing to its stouter form it has a median face in place of an edge, and upon this face, which is hollowed, is set the carpus. That joint, with the two which succeed it, forms a subcylindrical, tapering *palp,* which can be stretched out so as to be roughly in line with the axis of the basi-ischium and merus, but in the normal position is folded back against the hollow face of the merus. In this position the palps fill the gap which would otherwise be formed by the outward tilting of the merus, and thus complete the operculum.

As has been mentioned, the *mode of articulation of the joints* is that which is found in the legs. At the proximal end of each, the rim of the hard cuticle is raised, at two points on opposite sides, into articular processes which, bridging over the arthrodial membrane, play against corresponding surfaces on the distal rim of the preceding joint; and these articular surfaces are so shaped as to limit the movement of the distal of the two joints to a particular direction. Since, however, this plane is a different one in each joint, the limb as a whole has a good deal of mobility, though owing to its shape and position the third maxilliped is less freely movable than the legs. I have not thought it necessary to give details of the articulations of the several joints, but particulars of the movements they permit will be found below. They are modifications of those of the segments of the legs.

A remarkable feature of the third maxilliped is the way in which it is completely outlined with *hairs,* set along the edges of its flat surfaces. Most of these hairs are feathered in one way or another. They are short where the edge is, in the normal position, apposed to some other structure, but long on that part of the anterior (morphologically external) edge of the merus and carpus over which the gill-stream flows. Along the median edge of the ischium there run on the lower (ventrally-facing) side two narrow parallel bands of hairs with a naked, convex strip between them. These hairs are stout, with a close, stiff feathering on all sides. The actual edge is finely but bluntly toothed. On the inner or dorsal (morphologically anterior) side of this joint there is a row of hair-tufts near the median edge, and a rather sparse band of hairs near the outer edge. The dorsal side of each of the last three joints is covered with long, and stiff, serrated bristles. The epipodite is fringed on both edges with long hairs, and the ventral (hinder) surface of the flange of the coxa upon which it stands is very hairy. The flagellum of the exopodite bears a fringe of long, feathered hairs, many of them jointed. A more detailed description of the hair-system of this and other limbs of the Shore Crab is given by McIntosh (**11**). With its functions I will deal later.

The *cuticle* of the third maxilliped, except the flagellum and the blade of the epipodite, is hard and pigmented, like that of the rest of the exposed surfaces of the body. In this respect it contrasts strongly with that of the other mouth-parts.

The *muscular system* of the third maxilliped closely resembles that described by Pearson (**13**) for the same limb of the Edible Crab, and I have not examined it further than was necessary to assure me of this fact. Each of the joints of the limb has a flexor and an extensor muscle, those of the coxa and basi-ischium arising from the endophragmal skeleton and being inserted by conspicuous tendons, those of the remaining joints arising each from the joint preceding that upon which it is inserted. The exopodite has flexor and extensor muscles for the stem, which they enter from the coxa; but the flagellum has an extensor only, and must be brought back into the flexed position by its elasticity. The epipodite possesses muscles, but its most important movements are probably those which it carries out passively, under the action of the powerful muscles of the coxa.

The *action of the flexors and extensors* of the coxa is to draw the whole limb to and from the normal position, in which its median edge meets that of its fellow on the middle line. In moving outward it passes a little ventrally, so that it clears the sub-branchial region of the carapace. This movement at the same time uncovers both the mouth-field and the inhalent opening of the gill-chamber, and sweeps the epipodite under the gills, as I will explain later. The movements of the basi-ischium are more complex. They may be analysed into: (*a*) a movement to and from the middle line independently of the movement of the coxa, (*b*) a dorso-ventral rotation, like the letting down of a flap, (*c*) a rotation about a longitudinal axis on the outer side of the limb, like the opening of a door, (*d*) a divarication of endopodite from exopodite. This latter movement must be due to a contraction of the extensor muscle of the exopodite simultaneously with that of the flexors of the basi-ischium, for this bears the exopodite and tends to carry it in its own direction. The other movements of this joint are more difficult to understand, since they seem to take place with a good deal of independence, and the muscular apparatus does not appear to be adequate for this. Actually, they are performed together, combined into a single sweeping movement whose direction is decided by the form of the articulation between basi-ischium and coxa, but a compensating movement of the coxæ can keep the edges of the two limbs together, so that they are let down as a flap without at the same time necessarily opening as a pair of doors, though their planes are now directed obliquely and meet ventrally at an angle. The articulation is, moreover, not absolutely rigid, and the movements may therefore perhaps be modified by the small additional flexor muscle described by Pearson. The merus, of course, shares the movements with the basi-ischium, but it is capable of a moderate amount of rotation upon its articulation with the latter. The rotation is oblique, from within outwards and at the same time dorso-ventrally. It is not conspicuous in the living crab, but it is used sometimes to lower only the distal half of the operculum, and sometimes to give free play to the movements of the palp. The joints of that organ can move upon one another, but it is generally flexed or extended rather stiffly as a whole. It is so articulated that in extension it moves upwards as well as forwards. The flagellum of the exopodite is flicked outwards and inwards with very great rapidity, so that at times it cannot be followed by the eye. I have already alluded to the movements of the epipodite.

2. *The Second Maxilliped* resembles the third in general plan, but differs from it greatly in appearance on account of the following features:—It is smaller, and its cuticle is thinner. In the *endopodite*, the basi-ischiopodite is short and its components are easily recognizable, the merus is very long, and both, though flat, like the rest of the limb, are narrow. Actually they are narrower than the last three joints, which are more flattened than those of the third maxilliped. The *exopodite* is as large as that of the third maxilliped, and much longer than its own endopodite. It is grooved to fit against the edge of the branchiostegite. The *epipodite* is not hinged to the coxa, and a supporting rod of chitin runs from that joint along its anterior edge. It bears a long podobranch, and its distal part enters the gill-chamber, passes between its own arthrobranch and the anterior arthrobranch of the third maxilliped, and lies, like the epipodite of that limb, within the gills. The second maxilliped has the same *relations to the sternum and epimeral region* as the third, but is not connected with them by articulations like those of the latter limb.

The second maxilliped is not outlined with *hairs* like the third, but a good deal of long hair is developed upon it, especially on the hinder face of the basal joints, on the epipodite, along the outer and towards the end of the inner edge of the merus, at the end of each of the last three joints, and on the outer edge of the exopodite. The end of the last joint bears about eight very strong spines. The inner edge of the merus is not toothed. On the basal joints, and on the exopodite, the hairs are feathered.

The *musculature* of the second maxilliped resembles that of the third, but the limb is more mobile.

3. *The First Maxilliped* is a thin, flat limb, covered for the most part with delicate cuticle, from which the majority of the articulations have disappeared. The *coxa* is a short, broad region, whose entity is established by

the presence, on the anterior side, of a rod-like sclerite, which runs across it and at its median end expands into the stout cuticle of a large, subpyramidal endite. The apex of this endite is directed dorsally, towards the mouth, and that side of it which is opposed to the sternum forms a facet, above the membranous attachment of the limb. At its outer end, the transverse sclerite articulates with the stout cuticle at the base of the epipodite, and that in turn makes articulation by means of a hard process with the epimerite. I have not been able to find a true articulation on the inner side of the limb. The epipodite, which lies *outside* the gills, is much expanded at its proximal end, especially in a triangular forward lobe. A strong tendon runs along it. The *basipodite* is represented by a soft region distal to the coxa. It bears on the median side a large, flat, forwardly projecting endite or *lacinia*, which has a curved outer and a straight median edge, and is a little concave dorsally (anteriorly), so as to fit over the surface of the mandible. Distally the basis bears the *exopodite*, which resembles that of the second maxilliped, and the *endopodite*, which consists of an unjointed shaft, flattened in a plane which faces obliquely outward and inward, with a triangular distal expansion, flattened in an almost horizontal plane and separated from the shaft by a not very flexible suture. This expansion completes in front the exhalent channel of the gill-chamber. Its median edge is turned ventrally and lies against the anterior side of the mandible.

The limb is outlined with stout *cuticle*, which also passes along the sutures between the protopodite and the exopodite, endopodite, and endites. Its relation to the sternal and epimeral regions resembles that of the second maxilliped, but at the base of the epipodite there lies, as has been mentioned, a rather ill-developed articulation, which is not present in the limb behind it.

A row of long, flexible *hairs* follows the outer edge of the exopodite, the distal and inner edges of the endopodite, and the outer edge of the large endite. On the inner edge of this endite the hairs are more numerous, shorter, and rather stouter. The proximal endite is covered with long hairs, all directed towards the mouth. On the exopodite, the inner edge of the endopodite, and the outer edge of the large endite the hairs are feathered.

Flexor and extensor *muscles* of the coxa move the limb as a whole. The exopodite has a musculature like that of the third maxilliped, and the endites have muscles of their own. The epipodite has a system of three powerful muscles.

The limb can be *moved* to and from the middle line of the body, doubtless by means of the muscles of the coxa. In moving outwards it also travels a little backwards. The large endite makes independent movements, rotating forward-outwards and inward-backwards and thus with its edge describing an ellipse. Usually it moves inward-backwards towards the mouth when the rest of the limb is rotating outward-backwards, and thus the smaller endite, which projects towards the mouth, is being drawn away from the latter. When the smaller endite comes forward into the mouth the larger endite moves away from it.

4. *The Maxilla* (*Second Maxilla*) is a very broad limb, flattened in its distal parts, but with a swollen nucleus representing the main part of the *protopodite*. This region bears on the outer side the large, quadrant-shaped, slanting exopodite or scaphognathite, distally the roughly-ogival, peaked endopodite, and internally the two cleft *lobes*, representing four endites, which characterise the maxilla of the Decapoda. I have already (**5**) suggested that the first of these endites belongs to a precoxal segment of the limb, the second to the coxa, and the third and fourth to the basis. The first cleft lobe is in *Carcinus* reduced to a pair of narrow ribbons. The limb is covered with a delicate cuticle, thickened in places to form certain *sclerites*. Across the protopodite there runs on the ventral (morphologically posterior) face, from the junction between the cleft lobes to the base of the limb at its outer side, a raised ridge, strengthened by a sclerite which probably represents the coxa. At its outer end this abuts upon a longitudinal piece which caps the side of the swollen nucleus of the limb, and which is sutured to, but not definitely articulated with, the epimerite. More distally, the protopodite is crossed by an irregular **M**-shaped, transverse ridge, strengthened by two sclerites, each of the form of an inverted **V**, which are hinged to one another where they meet at the apex of the **M**. This appears to represent the distal limit of the basis. On the dorsal (anterior) face of the limb a longitudinal ridge, strengthened by a sclerite which roughly corresponds in position to the outer member of the **M** on the opposite face of the appendage, partly separates exopodite from protopodite. On the anterior face of the *scaphognathite* are two sheets of stout cuticle, with thickened edges, which support it and provide for the insertion of the accessory muscles. The maxilla is *seated* upon the membranous body-wall, in front of the sternum, upon which it does not abut. It is attached by membrane only, except at its outer end, where, as mentioned above, one of its sclerites is joined by a flexible suture to the epimeral region.

The *hairs* which in a prawn fringe the whole edge of the scaphognathite are here found at its anterior and posterior returning edges only. As in the prawn, they are feathered. The endopodite is fringed with long, silky hairs, but these are feathered only at the base of the outer edge. The ends of the cleft lobes bear relatively short, and, for the most part, simple hairs.

The swollen base of the maxilla harbours a complicated and relatively powerful *musculature*. According to Pearson (**13**), whose account is, I think, applicable to *Carcinus*, there are in *Cancer* two extensors and two flexors of the coxa, and four "extensors" and four "flexors" of the scaphognathite. It would perhaps be preferable to call these muscles abductors and adductors respectively, since they draw the limb downwards from the side of the body and upwards towards it. They arise from the endophragmal skeleton, and are inserted on the base of the scaphognathite. In its anterior part, the scaphognathite is crossed, at right angles to its long axis, by half-a-dozen bands of muscle, which, pulling downwards, curve its surface. These are the "accessory muscles." They arise from the sclerites of the basal portion of the limb, and are inserted on the anterior of those which support the scaphognathite. A feeble strand of muscle runs across the base of the endopodite to the second cleft lobe, but independent movements of these structures, if they take place at all, are insignificant.

The *movement* of the maxilla consists in a flapping of the scaphognathite to and from the roof of the exhalent passage of the gill-chamber. It is carried out in two ways, according as the current is being directed backward or forward. To drive the water forward, the posterior and outer end of the scaphognathite is smartly applied (presumably by the "outer flexors") to the roof. Then the accessory muscles, which have been keeping the organ curved, allow the flexors to bring the remainder of it into the same position, with the undulating movement described by Garstang (8). Finally, it is drawn downwards by the extensors, being at the same time curved by the accessory muscles, so that it becomes concave towards the roof. To drive the water backward this procedure is reversed. The bending of the scaphognathite which it involves is facilitated by the fact tnat the two supporting sclerites of that organ are united by a flexible region. It seems possible that the function of the muscles of the coxa is to hold firm the protopodite when the accessory muscles contract. The lobes of the median edge of the limb may be seen to be drawn passively to and fro with each stroke of the scaphognathite.

5. *The Maxillule* (*First Maxilla*) is a small limb, flattened and curved to fit against the surface of the mandible, and composed of three inwardly-directed lobes—the inner and outer laciniæ and the endopodite—and an external basal portion which unites them. It is usual to regard the laciniæ as representing the coxa and basis, but, as I have elsewhere argued (5), the *proximal lacinia* is probably the gnathobase, or endite of the true first segment of the Crustacean limb, "the 'precoxa' or 'pleuropodite,' which may or may not have originally existed as a free joint in every biramous limb, but has now nearly always disappeared, either by fusion with the trunk or with the second joint (coxa or coxopodite), or perhaps sometimes by excalation." In the maxilla it is represented by one of the components of the first cleft lobe. This lacinia is narrow and strong, and curves backward and dorsally to enter the mouth, at the hinder end of the mandible. Its base is widened and is continued across the face of the limb as a ridge, covered partly with thin cuticle but supported by a sclerite, and projecting anteriorly. Towards its outer end this ridge turns backwards (posteriorly), with a suture in the sclerite which supports it, and dies away upon the stout articular sclerite,

with which its sclerite makes a narrow articulation. The second segment of the limb, the true coxa, is represented by the region which connects the two laciniæ. For the most part it is covered with soft cuticle, but its outer side is strengthened by a stout bar, the *articular sclerite* just alluded to. This runs along the outer side of the basal portion of the limb. Proximally it articulates with a hard piece upon the epimeral region; near this it is joined by the sclerite of the precoxal ridge; distally it has a swelling with which the sclerite of the basipoditic (outer lacinial) ridge articulates. On this swelling stands a tuft of very long setæ, which may be called the "coxopoditic setæ." The *outer lacinia* is much larger than the inner, and its end is expanded and has roughly the same shape as the large distal endite of the first maxilliped. Like the inner lacinia it is prolonged as a ridge across the face of the limb, but the ridge has no projection of its anterior edge and its sclerite makes a better articulation with the articular sclerite. It represents the basipodite. The *endopodite* has a wide base and a narrow, strap-like, blunt-ended continuation, separated by a suture. When the limb is *in situ*, this strap passes in a remarkable way over the shoulder of the mandible, lying in a notch, much as the endopodite of the maxillule of the Prawn is carried in a notch on the edge of the metastoma.

The maxillule is *attached* in a little depression of the body-wall immediately behind the mandible. Like the maxilla it does not abut upon the sternum. It has an external but not a median articulation.

Besides the coxopoditic setæ, which are very long, strong, and thread-like, the limb bears on the outside of the endopodite a small patch of feathered *hairs*, at the end of the endopodite another such patch, and on the inner edge of the endopodite a fringe of long silky hairs. The laciniæ bear on their free ends a mass of very strong spines, which on the tip of the inner lacinia are curved in the same direction as the lacinia itself. The *cuticle* of the endopodite and basal region is thin, but on the laciniæ and their ridges and the articular sclerite it is of considerable strength.

Pearson (**13**) describes in the maxillule of *Cancer* four muscles—two outer and two inner, a "flexor" and an "extensor" in each pair, the flexors arising from the protogastric region of the carapace and the extensors from the endopleurites of the endophragmal skeleton. In *Carcinus* six strands of muscle enter the maxillule. Of these, two are inserted on the articular sclerite, one at each end of the sclerite of the outer lacinia, and two on the sclerite of the inner lacinia, at the base and near the middle. This set of muscles appears to be adapted to move the whole appendage inward and outward, and to rock each lacinia to and fro in an antero-posterior direction. There is also a band of muscle running from the sclerite of the outer lacinia to the middle of the broad part of the endopodite. I believe that this when it contracts pulls the lacinia forwards towards the endopodite, which is firmly strapped to the mandible by its narrow end.

The laciniæ are capable of independent *movement*. The outer moves to and from the middle line and also forwards and backwards in the body, and it combines these movements in varying degrees. The inner moves in and out of the mouth.

6. The *Mandible* is a short limb, whose proximal region or *body* is widened athwart the body of the crab and very strongly calcified. This region, which may represent either the coxa or precoxa, but is more probably both combined, is divided into two portions which it is convenient to know as the "head" and the "apophysis." The junction between these is marked by deep notches on the anterior and hinder sides and by an oblique, inflexible suture which joins them. The *apophysis* appears to run deep into the body, but it is in reality not internal like the pieces of the endophragmal skeleton but an external structure, the true base of the limb, which pushes in the membranous body-wall till it comes to lie in a deep, close-fitting pocket. It presents to this pocket a convex anterior face and to the interior of the body a deeply concave posterior face. Upon its edges are inserted the muscles which move the limb. The *head* is much deeper from before backwards than the apophysis, and convex ventrally. It expands towards the middle line, where it presents to its fellow a sharp cutting or "incisor" edge, in the middle of which is an obsolescent tooth. Dorsal to the cutting-edge, in its concavity, is a low mound, the "molar process." External to this, also on the dorsal side, is a process with an outwardly facing concavity which articulates with a knob on the epistome. External to the articular process, and still on the dorsal face of the limb, is inserted the *palp*, an inwardly-curved structure, which should be composed of three joints but actually has only two, because the first and second have fused. In the normal position it is folded back above the limb and almost hidden. The joints of the palp are flattened, the second more than the first. The limb articulates in front with the epistome, and behind is flexibly sutured to the sclerite which supports the metastoma.

External to the base of the palp is a group of feathered *hairs*. The palp itself is bordered with rather long hairs, which are feathered at its base but stout and simple at its apex. There is also a patch of sparse hairs on the ventral face of the apophysis.

The *musculature* of the mandible resembles that described for *Cancer* by Pearson. There are four muscles. A large outer adductor, inserted by a broad tendon upon the outer angle of the apophysis, arises from the subhepatic region of the carapace, and by its contraction must pull the end of the apophysis downwards and so bring its cutting-edge upwards and inwards against that of the other mandible. An inner adductor arising from the dorsal carapace is inserted by a very long tendon near the inner end of the mandible, which it must pull directly upwards. Two abductors, inserted respectively near the outer angle and on the posterior border of the apophysis, will pull that part of the limb upwards and so rotate the cutting-edge downwards and outwards.

The sole *movement* of the head of the mandible is a rotation upon its articulation which alternately parts the incisor edges, opening them like a pair of doors, and brings them together. The palp is extended and flexed, digging its apex into the space between the incisor edge and the flank of the labrum.

7. *The Metastoma* is a fleshy structure which lies behind the mouth, between the mandibles and the maxillules. It has two forwardly-directed lobes, the *paragnatha*, which stand wide apart against the mandibles, covering the notches on the hinder side of the latter between the head and the apophysis. The paragnatha are joined by a low transverse cushion, a little raised in the middle, on the border of the mouth. The whole is supported on each side by a sclerite which follows its base and at the end is sutured to the mandibles. The paragnatha contain some glandular tissue, but are not muscular and appear to be moved only passively.

8. *The Labrum* is a large, fleshy lobe which forms the anterior border of the mouth. Its *base* is rounded and swollen in front but narrows behind, where it projects into the mouth. Distally it is produced behind into a *nose-like process* which overhangs the mouth. Its exposed (ventral) wall is strengthened by a triangular sclerite. Its sides are moulded to fit closely against the dorsal faces of the mandibles when the palps are flexed against them. It contains, besides a good deal of glandular tissue, much *muscle*, notably in two longitudinal bands. Its movements are hard to observe, since it has not so sharp an outline as the limbs and is only exposed when the mandibles part, but they appear to consist chiefly in a tucking of the nose into the mouth and its withdrawal.

9. *The Mouth* lies above the hinder end of the mandibles. It is a longitudinal slit, which forks in front owing to the projection into it of the base of the labrum, and behind owing to the low median prominence of the metastoma. To it converge all the surrounding structures—the nose of the labrum, the mandibular palps, the inflected hinder angle of the incisor edge of the mandible, the inner lacinia of the maxillule, and the pyramidal endite of the first maxilliped. All these are so formed as to make entry to the mouth easy but egress from it very difficult.

III.

1. *The functions of the mouth-parts* are threefold. They subserve respiration by keeping a stream of water flowing through the gill-chamber and hindering particles from lodging upon the gills ; they subserve alimentation by tearing up the food and thrusting it into the mouth ; and one of them, the third maxillipeds, cleans the eyes, antennules, and antennæ.

2. *The branchial chamber* of the crab is no less complex and specialized

than the rest of the organisation of that animal. In its widest sense, the term may be applied to the whole of the very large space that lies between the flank of the body and the over-arching fold of the carapace known as the branchiostegite, which encloses the chamber above, and without, and partly below. The flank itself constitutes the inner wall of the chamber. Of the two layers which compose the branchiostegal fold, the outer is hard and calcified, that which is towards the chamber is membranous. In their hinder region the two layers are not widely separated, and there are between them only blood-vessels and connective tissue; but anteriorly certain viscera intrude into the upper part of the fold. The hard layer of the branchiostegite lies at first almost horizontal, so as to form a roof above the chamber and the intruding viscera. It is then turned downwards at an angle, which in the hinder region is obtuse but becomes more and more acute as it is followed forwards, to form a wall which curves inwards till it reaches the flank of the body above the bases of the limbs. As the angle at which this wall joins the roof becomes more acute, the wall faces more downwards, till in the fore part of the body a portion of it becomes horizontal; there it forms a floor to the chamber. The shape of the chamber is of course determined not by the contour of the outer layer of the branchiostegite, but by that of the inner. This layer makes in the hinder part of the thorax a continuous curve from above downwards, constituting an arched inner roof to the chamber, which has here no floor properly so called. In front, however, where the outer wall becomes horizontal, the inner wall turns inward at an angle to line the floor of the chamber. In the thoracic part of the latter, the floor underlies the overhanging part of certain gills which project considerably above the bases of the limbs. In the head, it closes from below the exhalent chamber shortly to be described. A number of "dorso-ventral muscles" enable the membranous roof to be raised or lowered.

The chamber is sharply divided into two parts—a true "gill-chamber" in the thoracic region, and an "exhalent passage" or "prebranchial chamber" in the cephalic region. Of these divisions the *gill-chamber* is much the larger in every dimension. Its inner wall is battered back so as to face upwards as well as outwards, and is brittle, though thin, and composed of broad ribs —the so-called "epimera"—one to each limb from the last leg to the second maxilliped inclusive. That which lies above the cheliped is larger than the rest and prominent. Those behind it face a little backwards and those in front face forwards, so that the whole wall is convex outwards, forming a low, roughly half-conical mound. In front, the chamber narrows rapidly, its membranous roof at the same time falling steeply to the hinder opening of the *exhalent passage*, where the roof is upheld, and the opening maintained, by an arching, calcified sclerite. Here the roof turns forward as that of the exhalent passage. This is a shallow chamber which diminishes in width as the carapace narrows forwards. Its inner wall has become merged in the roof, so that it has only roof and floor. Shallow though this channel is, the effective depth of its entrance is lessened by a double barrier. One component of this is the epipodite of the first maxilliped, which, sweeping round on its spiral course, roughly parallel with the epipodite of the third maxilliped but starting in front of the gills and lying upon their outer surface, crosses the portal of the exhalent passage in such a way as to bar it from behind and from outside and leave access to it only from above and from within. Since the wide base of the epipodite does not merely touch the floor with its edge but lies flat against it, the movements by which the tail is caused to travel over the gills probably never separate the base from the wall of the passage. The other component of the barrier is the "branchial ridge" of Pearson, a fold of the membranous layer of the floor, parallel with the anterior side of the principal inhalent opening but at a short distance from it, which fits between the podobranch of the second maxilliped and the epipodite of the first and helps to enable the latter to make effective contact with the floor. On the inner side of the exhalent passage, the edge of the branchiostegite does not meet the body closely at the bases of the limbs, but leaves there a long, narrow gap. This is normally filled by the endopodite and exopodite of the first maxilliped and the exopodite of the second, which are moulded longitudinally to fit together and against the mandible and to receive the branchiostegite. Further forward, in front of the mandible, the body-wall, which is here the hinder part (endostome) of the epistome, is concave, and so falls away dorsalwards from the branchiostegite and widens the gap. Thus is formed the *exhalent opening.* It is bordered behind, and contracted, by the expanded end of the endopodite of the first maxilliped, and discharges forwards and towards the middle line, so as to direct the current of its side to the antenna and eye of the opposite side.

The *gills* of *Carcinus* are nine on each side. The second maxilliped has a podobranch and an arthrobranch, the third a podobranch and two arthrobranchs, the cheliped two arthrobranchs, and the first and second walking-legs each a pleurobranch. Each gill is a tapering structure. Except the podobranch of the second maxilliped, which lies horizontally and is directed backwards at the bases of the maxillipeds in front of the principal inhalent opening, the gills are turned upwards and inwards, and lie against the inner walls of the chamber, converging to its highest point, just before the roof falls in front. They are closely applied to one another and separate a shallow "hypobranchial space" against the inner wall from an "epibranchial space" under the branchiostegites. The gills are phyllobranchs. Each of them, save the arthrobranch of the second maxilliped, is heart-shaped in transverse section, owing to the fact that the leaflets project as lobes above the axis but die into it below. Thus it comes about that where two gills lie side by side there is between them on the under side a "hypobranchial channel," and above each of them is an "epibranchial channel" along the axis, between the leaflets. The arthrobranch of the second maxilliped has leaflets on the posterior side only, the anterior side, which is applied to the wall of the chamber, being flat; but along its edge an epibranchial channel runs as a gutter. The hypobranchial channels are part of the hypobranchial space and are in communication with one another under the gills, especially at the bases of the latter, which are there a little arched, leaving a longitudinal corridor in which lies normally the epipodite of the third maxilliped. The epibranchial channels are part of the epibranchial space, and will communicate over the gills unless the roof be lowered on to the latter. At the hinder end of the chamber there is a space which contains no gills. This space is very shallow and in it lies the enigmatical fold of the body-wall known as the "pericardial lobe." It is shielded from the current entering over the last leg by a ridge which, as I shall presently show, directs the water forwards and downwards, and it probably plays no important part in the circulation of the water about the gills. The branchiostegite fits closely against the bases of the gills, which are flattened back to receive it. Above most of the rest of the surface of the gills the epibranchial space is probably as a rule deep enough to allow the epipodite of the first maxilliped to play freely, but by the action of the dorso-ventral muscles varies in depth from time to time owing to circumstances of which nothing is known, and which may be related to other functions than respiration. At the anterior end of the chamber, where the arthrobranchs of the third maxilliped and cheliped face partly forwards towards the roof as it falls to the opening of the exhalent channel, there is a deeper part of the cavity. Since its roof is flexible like that of the rest of the epibranchial space, it is possible that this does not always exist, but I have always found it, and I believe that it is kept in being, in its lower part at least, by the attachment of the roof to the arched sclerite that I have mentioned. It slants downwards, forwards, and outwards to the opening of the exhalent channel. From it water must be drawn by the action of the scaphognathite into the exhalent channel, which, as I have shown, cannot receive water from the region directly behind itself. Thus the water from all parts of the chamber must pass through this space, and, though it is not sharply defined from the rest of the epibranchial space, it may be distinguished as the "collecting space."

The gill stream *. The water which bathes the gills normally makes *entry* under the edge of the branchiostegite in the thoracic region and leaves in the same way in the preoral region. According to the classical account of this process, given by Milne-Edwards (**12**), the entry of the water takes place only by an opening which lies in front of the coxa of the cheliped and

* It was not till I had written the paragraphs on this subject that I saw the paper of Mr. R. K. S. Lim, published in 1918 (**10**). As my work extends as well as confirms that of Mr. Lim, I have left unaltered what I had written.

external to that of the third maxilliped. Other authors (Bell (1), Giard (7), Bohn (2, 4)) have stated that the water enters above the legs along the whole length of the carapace behind the third maxilliped. Pearson, however (13), finds that in *Cancer* entry is made principally by an anterior opening, which is that of Milne-Edwards, and secondarily by a posterior opening above the last leg, but not between these apertures. An examination of the structures which adjoin the edge of the carapace in *Carcinus* shows (1) a relatively large opening in the position indicated by Milne-Edwards, (2) a smaller opening above each leg, the cheliped included. The openings above the first three walking-legs are separated from one another by meetings between the prominences upon the flank with which the legs articulate and corresponding prominences of the branchiostegal edge. They are longitudinal, and slit-like but well formed. That above the last leg is very narrow, and imperfectly separated from the one in front of it*, and that above the cheliped is separated from the opening of Milne-Edwards only by a close fitting of the branchiostegite to the coxopodite when the limb is turned forwards. Access to each of the openings above the legs is obtained principally between its coxopodite and that behind it, and by moving the leg backward and upward the crab can almost close it, though at the same time the approach to the orifice above the leg next in front is more widely opened. A large hairy tract on the under face of the branchiostegite has no doubt the function of filtering the water which is drawn through it towards the inhalent openings, and especially that of Milne-Edwards. It rises into a long fringe around a bare patch where the cheliped lies against the branchiostegite, and is there met by fringes on the borders of the cheliped so as to form what is probably a very efficient guard for Milne-Edwards's opening. Along the edge of the branchiostegite another long fringe forms a similar protection for the openings above the legs. By placing with a pipette against each opening a little carmine suspended in sea-water, it may be seen that water enters at all of them, even when the third maxillipeds are opposed so as partly to close with their epipodites Milne-Edwards's opening, and that the water from any opening takes a little longer to reach the exhalent orifice than that from the openings in front of it. When the third maxilliped is divaricated from its fellow, so as to open widely the aperture of Milne-Edwards, water enters there more freely, passing forwards as well as backwards, since the anterior side of the opening is now uncovered, and bathing very copiously the podobranch of the third maxilliped, which has been drawn backward into the full stream. That

* The crevice above the last leg is continuous with that between the hinder edge of the carapace and the first abdominal segment. Narrow though this opening is, the state of the hairs which line it shows that a little water enters it. No doubt this water flows both ways towards the two gill-chambers. The occasional presence of a little mud in the middle chamber which is connected with the hinder crevice of the carapace proves that water must enter it also, though probably it does not there perform any important function.

podobranch may thus have a greater physiological importance than its size would suggest, though it seems doubtful whether in its more isolated position the water would be drawn between its leaflets. The divarication of the third maxilliped also exposes an opening between it and the limb in front of it which helps to admit water to the fore part of the chamber.

The course of the water within the gill-chamber is more difficult to follow, but there can be no doubt that on entering, it passes *under* the gills, that is into the hypobranchial space, then comes outwards between the gill leaflets into the epibranchial space, and finally flows by way of the collecting-space into the exhalent passage. That practically all the water which enters the gill-chamber takes this course, and does not pass directly from the exterior to the epibranchial space, I am convinced by the following considerations :—(1) It is exceedingly unlikely that the blood in the leaflets of the gills is exposed to the stream of water only on their edges, and that their flat surfaces are dependent on eddies or diffusion for the renewal of the water in contact with them. (2) When carmine is caused to enter through any of the openings it is found principally, and the large particles are always found, underneath the gills. (3) The disposition of the parts is such as to suggest that the current flows in the direction that I have described. From each of the openings behind that of Milne-Edwards the shortest route to the exhalent passage leads under and through the gills. If there were a wide space between the gills and the border of the branchiostegite, the resistance due to friction with the leaflets might cause the water to pass over the gills, but actually the branchiostegite fits, as has been said, close against the gill-bases. In front of the cheliped the relations of the parts are different. Here, when the third maxilliped is in its normal position, its coxa and epipodite bar the passage of the water forwards and direct it inwards under the gills; but when the maxilliped is divaricated, the shortest route to the inhalent channel would be, were it not for the barrier formed by the epipodite of the first maxilliped, directly forward. It would then pass partly through the podobranch of the second maxilliped, but in great part between that structure and the floor of the chamber or the bases of the other gills, and would not be distributed to the latter organs, which lie above the direct course. Actually, however, the existence of the barrier mentioned must prevent the water from being chiefly drawn in this direction and cause it to circulate through the upper gills. That the water does actually take the route through the gills can easily be seen by cutting a window in the floor of the exhalent passage and placing carmine in Milne-Edwards's opening. The carmine will be found always to pass under the gills and to reappear above the scaphognathite, not to take the direct route.

The water which enters above the first and second walking-legs flows forwards and inwards along a shallow gutter hollowed on the epimerite *till it reaches the entry of a hypobranchial channel* between the pleurobranch of its leg and the gill which adjoins it in front ; and through this it passes into the hypobranchial space. The water which enters the opening behind the cheliped flows similarly forward over the arthrodial membrane, which is shaped to provide a kind of duct for it, to the entry of the hypobranchial channel between the anterior arthrobranch of the cheliped and the posterior arthrobranch of the third maxilliped*. At this very large portal of the hypobranchial space it meets the water from Milne-Edwards's opening. From that aperture the current passes, when the third maxillipeds are opposed, obliquely backwards through the portal just mentioned, though a little may stray forwards to pass between the arthrobranchs of the third maxilliped. When, however, the maxilliped is divaricated and the opening thus fully uncovered, water passes also to the channels between the arthrobranchs of the third and second maxillipeds, and to the podobranchs of those limbs. The water which enters the opening behind the last leg is prevented from flowing directly forwards by a ridge on the epimeral region, passes over the articulation of the last leg, which is not prominent like the others, joins the stream which enters between the last two legs, and reaches the hypobranchial space by passing forwards through a definite entrance formed by the shaping of the hinder leaflets of the last gill at a spot near its base and at the end of the longitudinal corridor mentioned above. The arrangements may be summed up by the statement that the water which enters over each limb passes into the hypobranchial space by an opening between its gill and the gill of the limb in front of it, except that most of the water entering above the third maxilliped passes behind its gills.

In each hypobranchial channel, the water flows, I believe, upwards, mingling to some extent under the gills with that in the adjacent channels, and diminishing as it goes by loss between the leaflets of the gills to the epibranchial space. Since this loss is hindered by friction against the leaflets, the water does not all escape till the top of the gills is reached, and is thus distributed over as wide a gill-surface as possible.

The course of the water *over the outer surface of the gills* presents a very difficult problem. The shape of the chamber gives no convincing indication of the direction in which the stream gets through it, and its size, as a whole and in each part, depends upon the changing form of its roof. I can only offer some suggestions on this subject.

Normally, the water will pass direct from the point at which it issues from between the leaflets of the gills to the collecting-space. If, however, the roof be lowered on to the surface of any part of the gills, the water which is passing through them is probably got away by the epibranchial channels. The appearance of these structures strongly suggests that a current flows

* The entry to the hypobranchial channel between the arthrobranchs of the cheliped is very small, and that channel probably receives its water from the longitudinal corridor.

along them. They widen from above downward, and it would at first seem as if the current must flow in that direction. But (1) as each channel widens it grows shallower, so that its capacity is no greater, but rather less ; (2) its lower end is probably closed by the edge of the branchiostegite, and in any case leads to a part of the chamber that does not directly communicate with the exhalent passage; and (3) the direction of the leaflets is such as at the lower end to cast the water into the channel in an upward direction. It is therefore probable that the current flows upwards. On the other hand, near the upper end the channel narrows so much that its capacity is greatly diminished, and here the water must be overflowing from it into the space over the gills, which is near the top of the collecting-space. The grooves between the convex surfaces of adjoining gills, which may be known as "interbranchial channels," form a similar system.

All the *water enters the exhalent passage* from above and within—that is, from the collecting-space. This is due partly to the fact that, as has already been shown, access to the passage from behind is barred, and partly to the fact that the stroke of the scaphognathite is made from below upwards, against the roof ; and, as has also been shown, it has the important effect of causing the water to flow through instead of over the gills.

The working of the scaphognathite has already been described. The effective stroke is the upward one, but the downstroke must act upon the water which has entered the lower part of the passage during the upstroke. Probably the bulk of this is driven into the collecting-space and a small portion sent forward to the exhalent orifice.

The stream that issues from each branchial chamber is directed, as has been said, obliquely across the epistome to the opposite side of the front, and often it does in fact take that course. But normally it meets in the middle line the current of the other chamber, and the two deflect one another so that they flow forwards under the antennules. A further modification of the direction of the current is brought about by the activity of the flagella of the maxillipeds. Flicking to and fro extremely rapidly, these exert their force more on the outward stroke when they are drawn by their extensors in the direction of their concavity as a cilium moves than when they are returning by their own elasticity in the direction of their convex sides. They not only reinforce the current very notably, but also turn it outward, and in particular, I think, by means of the hairs with which they are fringed they draw away particles which might otherwise lodge upon the organs of special sense.

The regulation of the gill-stream is brought about in two ways—by alterations in the size of the openings, and by changes in the beat of the scaphognathite and the exopodites of the maxillipeds. I have already shown how the flow through the anterior inhalent opening is regulated by the third maxilliped, and how the legs can close the openings which lie behind them. The size and form of the exhalent opening must also have an important influence on the current. The aperture is smallest when the third maxillipeds are closely opposed. At such times a steady stream issues from the opening which they leave in the middle of the epistome and flows forwards under the antennules. When a wider opening is necessary, either to provide for a greater flow or to allow the current to be directed to the sides of the body, the operculum may be opened in varying degrees by lowering either the meri only or also the basi-ischia. At such times the form of the exhalent opening proper may be modified by alterations in the position of the expanded end of the endopodite of the first maxilliped.

The function of the epipodites * is the cleaning of the gills. Moving to and fro over the gill-surface they brush it, drag over it their long, flexible, barbed hairs, and thus prevent particles that are brought in by the gill-stream from settling there and closing the minute passages between the leaflets. The importance of this function is shown by an observation of Pearson, who found that in a crab in which the epipodite of one of the first maxillipeds had been destroyed, the outer surface of the gills of its side was covered with a layer of fine mud. In one of my crabs there was a similar deposit of fine sandy particles. In this case the epipodite was intact, but I have no doubt that it was in some way paralyzed †.

By an admirable mechanism the three epipodites, between them, reach almost every part of the gills. The epipodite of the first maxilliped lies *above* the gills and sweeps their outer surface. It is probably moved more by the action of its own powerful muscles than by the excursions of the maxilliped as a whole, which are not extensive, and if they were so would interfere with the other functions of the limb. This epipodite is very flexible, and, doubtless by the action of its muscles, it is kept closely applied to the rounded surface of the gill-mound while it swings upwards and downwards over the gills, describing an arc with its tip. In an almost vertical position it stands against the forward face of the mound. The epipodites of the second and third maxillipeds lie below the gills and sweep the inner surface of the latter. Both are stiffer than that of the first maxilliped. The principal movements of each are probably those which it undergoes passively with the coxa of its limb. These movements can easily be imitated upon a dead specimen, and they must occur with each of the excursions which the limbs are constantly making in life. The epipodite of the second maxilliped lies on the anterior, forwardly-facing region of the inner wall of the gill-chamber. When the maxilliped swings outwards, pivoting on its attachment, the epipodite makes a corresponding inward movement over the face of the thoracic wall, sweeping the inner surfaces of the gills that stand there, with

* The epipodites of the first and third maxillipeds have also the passive function of directing with their bases the course of the currents in the way that I have already described.

† Since the foreign matter was *above* the gills, it had presumably been brought in during reversals of the current.

which it is almost or quite in contact. As the maxilliped returns, the epipodite is drawn back to its former position. The epipodite of the third maxilliped reaches over the epimeron of the cheliped to lie against the posterior region of the inner wall. When the maxilliped is in the normal position the epipodite lies in the longitudinal corridor at the base of the gills. If the movement of the limb were simply outward, and if the epipodite were not hinged to it, the effect of its divarication from its fellow would be merely to press the epipodite more firmly inward against the wall above the bases of the gills, with which it would therefore tend not to be in close contact. Actually, however, the maxilliped, as I have stated above, rotates downwards as well as outwards, and thus moves its epipodite upwards over the flank of the body, while the movement presently brings the stout base of the epipodite against the articulation of the cheliped, and this opposition flexes it at its hinge and directs it outward as well as upward. Thus when the maxilliped is divaricated, the blade of its epipodite moves upwards and presses outwards against the under surface of the gills, which it sweeps and lifts a little from the thoracic wall, thereby flushing these parts with water. As the maxilliped returns to the normal position, the base of the epipodite is pressed against the arthrobranchs of the cheliped, and thus bent back into the longitudinal direction. The position of the epipodite of the second maxilliped upon the forwardly-facing epimera makes unnecessary any such special mechanism to bring it against the inner surface of the gills.

No doubt the movements of the epipodites have the effect of mingling and distributing the water in the gill-chamber while they clean the gills, but it is not clear that this has any such physiological importance as has been attributed to it.

The variations of the gill-stream are a very striking feature of the physiology of the crab. They may be studied either by the carmine method or by watching the movements of the flagella of the exopodites of the maxillipeds, and, after making a window in the branchiostegite, those of the scaphognathite. Since the latter method studies directly the working of the principal agent, it is the most instructive, though it is open to the obvious objection that the action of the scaphognathite is affected by the operation. But when the shock of the latter has passed off, its effects are less serious than might be expected. The most remarkable feature of the action of the scaphognathite is its extreme sensitiveness. Any rough or sudden handling of the crab is liable to cause it to stop—in the face of danger the creature holds its breath. Yet this does not always happen when it is expected. Other variations are brought about by less obvious causes. The scaphognathites work independently, and either of them may cease working while the other continues. Their beating changes its rate and force from time to time in the same individual, and differs in different individuals in the same vessel at the same time. Clearly the causes are sometimes internal: probably they are often external. From some observations of Bohn (4) on the reversal of the stroke it would appear that the crab is sensitive to changes both in the oxygen-content and in the carbon-dioxide-content of the water. Whether these circumstances act by altering the composition of the blood, or through the sense-organs, or in both ways is not clear. I would hazard a surmise that the third of these alternatives is correct, and from some casual observations I suspect that the antennules are sensitive to oxygen. Changes in the activities of the scaphognathite are accompanied, and its working facilitated, by actions of the subsidiary parts of the apparatus. Probably in the normal, quiet breathing of a resting crab, when the water is clear and perfectly oxygenated, the third maxillipeds are opposed and the flagella of the exopodites at rest. Most commonly, however, at least in experimental conditions, the crab sits with its maxillipeds lowered to some extent. This must have the advantage of lessening the work of the scaphognathite, when a considerable volume of water is being dealt with, by allowing it to get away with less friction ; and it also enables the flagella to be brought into play, both to help the scaphognathite, and to drive the current and its contained particles outward, away from the sense-organs. Like the scaphognathite, the flagella may work on one side only or on both at once. One, two, or three of them may work at the same time on each side, and they may give a single stroke or work continuously for long periods. The flagella of one side are complemental to the scaphognathite of the other, driving the current in the same direction, and I have not seen the flagella and scaphognathite of one side both at work while on the other side both are at rest. Further, the maxillipeds may be divaricated. This admits more water to the gill-chamber, admits it where it has a relatively short distance to travel and hence causes relatively little increase in work, and also supplies a set of gills which are out of the main stream when the maxillipeds are apposed. Changes in the posture of the crab have also, as Bohn has pointed out, an effect upon the work of the scaphognathite. When the water is clean and well oxygenated, a horizontal position is possible, though there is always some upcast, at least when the maxillipeds are opposed. But when the water is muddy or foul, the vertical position is necessary to enable reversal of the current to obtain more oxygen, as will presently be shown. The exhalent opening is then often above the surface, and work is heavier while the flow is forward. From time to time the third and second maxillipeds make violent excursions outwards. This happens more frequently when the water is not clear, and it has the effect of sweeping the gills with the epipodites.

From time to time also, the scaphognathite reverses its action, and for a shorter or longer period draws water in at the exhalent opening and drives it backward through the gills and out at the inhalent opening. This is done when foreign particles or distasteful substances are being drawn in, and it is noticeable in carmine experiments when the particles are too coarse. Its function in this case is obvious. But it also happens at intervals when the water is quite clear and pure. It probably then drives out particles which have gradually accumulated under the gills while the current was flowing in the forward direction and which would in course of time prove harmful. The reversal of the current, which was first studied by Garstang (8, 9) in *Corystes* and other genera, has been examined in *Carcinus* by Bohn (2, 4), who has shown that it always takes place, but varies in frequency and duration with the foulness of and amount of matter in suspension in the water, and that when the water is chemically foul the crab will raise the normally exhalent opening to the surface so that it draws in either the better oxygenated water of the surface or air, which passes out in bubbles at the opening of Milne-Edwards after oxygenating the water in the chamber. These results I can confirm from my own observation. The crabs will live in exceedingly foul water if they be permitted to raise the front of the body out of it, but may be asphyxiated by preventing this. Bohn (4) thinks that the reversal of the scaphognathite has an advantage in resting its muscles. I am not clear that it is necessary to suppose that it has any other function than that of cleaning the chamber and enabling the animal to obtain a better supply of oxygen.

3. In *feeding*, the crab severs the food into morsels which it swallows without finely dividing them. It always seizes the food with the chelæ. The third maxillipeds then part, and the food is placed by the chelæ between the mandibles. If the mass of it be very bulky, one or more of the legs may be brought into action to assist in lifting it and thrusting it towards the mouth. The mandibles part to receive the food, and then close upon it. They do not cut it by a slicing action or chew it, but unless it be soft enough for them at once to sever a morsel of it by pressure, they hold it firm while it is being divided by the action of other organs. If the food be very soft, they may even sometimes be seen to be held wide apart while it is thrust into the mouth by the action of their palps and of the nose of the labrum. Usually, however, the food (I have fed my crabs upon various parts of the body of fishes and upon meat) requires the assistance of other organs for its severance. In this case it is torn by being pulled outwards from the mandibles, much as a crust may be torn by being held with the teeth while the hand wrenches a part of it away. The outward pull is sometimes given by the chelæ, especially if the mass of food be tough, and they often keep a hold upon it when they do not appear actually to be pulling; but most often the work is done by the third maxillipeds, which grasp the food by pressing upon it with the toothed inner edges of their ischiopods and at the same time press downwards upon it with their palps, somewhat as the digit of a subchela is closed. These limbs do not cut or chew the food, and rarely pass it towards the mouth, but by pulling it outwards tear from it the portion which is held by the mandibles. The second maxillipeds work in various ways, and their action, like that of the organs in front of them, is often hard

to follow because they are hidden by the third maxillipeds. After the removal of the latter, movements of the inner jaws may be observed, but I have not been able to induce crabs which have been so operated upon to feed *, and in any case their feeding would not be normal. The second maxillipeds apply to the food their last joints, armed with the strong spines which have been mentioned. With these they sometimes thrust outwards, aiding the third maxillipeds or, if the morsel be small, even taking their place. At other times they appear to be thrusting the food inwards, towards the gape of the mandibles, at others to work up and down upon it, strained as it is between the third maxillipeds and the mandibles, so as to cut through it. It is difficult to discover what is the work of the first maxilliped. The action of the great laciniæ would suggest that they are cutting the strand of food, but their armature of bristles is so much feebler than the arrangement of spines upon the dactylopodites of the second maxillipeds and on the laciniæ of the maxillule as to throw doubt upon the correctness of this impression. In view of the alternation of their action with that of the pyramidal endites, it seems possible that they are really brushing the frayed portions and fragments of the food backwards towards the opening of the mouth, into which the pyramidal endites help to thrust it. The shape of these endites and of the hairs upon them are such as to make it easy for the food to pass between them into the mouth, but difficult for it to emerge. The maxillæ are, I think, quite useless as jaws. Their distal lobes, at least, are feeble, inefficient structures, drawn passively to and fro with the strokes of the scaphognathite. I am less certain about the proximal lobes, but if these have a function I am unable to suggest what it may be. The maxillules are important and relatively powerful structures. I have described the movements of their laciniæ. The outer of these cuts at the food with its powerful bristles and the inner, I think, thrusts it into the mouth. Probably in doing so it is cutting or tearing it from the main mass. The paragnatha appear to have the function of closing the notches on the hinder edge of the mandibles, through which the food might work outwards, and of pouring upon it the secretions of their glands, whatever be the functions of these. I have already described the working of the mandibles. I am unable to see that their "molar" faces have any grinding action, but they appear to help to wall in the food which is being thrust into the mouth by the palps, and especially by the action and powerful nose of the labrum. I have been a little surprised, in feeding to the crabs portions of fish and meat containing bone which I should have expected them to be able to crush, to observe that they were rejected, sometimes after being stripped of the softer tissues. It is quite possible, however, that in other circumstances these would have been devoured. After the meal a flurry of the mouth-parts is usually to be seen.

* Possibly reflexes from these limbs are needed to co-ordinate the movements of the other mouth-parts. A prawn will as readily take food from a pair of forceps as from its own chelæ. A crab will not.

By brushing their various hairy surfaces against one another they detach the small particles of food that are clinging to them, and these are swept away by strong currents set up by the activity of the exopodites of the maxillipeds.

The *opercular function of the third maxillipeds* deserves mention here. The operculum is not of importance to the crab on account of any part that it plays in feeding. It is freely open during that process, and is not closed again till the mouth-parts have cleaned themselves. It undoubtedly protects the more delicate organs within it, as may be seen by the way in which it is closed when they are approached by any implement. But the closeness of its fitting, and its fringe of hairs, indicate that it is also a part of the respiratory apparatus. The current set up by the scaphognathite is a wonderfully strong one, partly because it is working in a closed system of passages, and there are several places in the neighbourhood of the inner mouth-parts where leakage is probably liable to take place, and throw unnecessary work upon the scaphognathite in keeping up a current of the swiftness which is needed. The closing of the operculum prevents this.

4. *The hairs* which are arranged in so definite a manner upon the limbs play no insignificant part in the events which have just been described. They are of an immense variety. A few particulars about them have been given above, in the course of the descriptions of the limbs, but it is quite impossible to do justice to this subject without devoting to it a special investigation. McIntosh (**11**) has examined their structure in detail, but their functions still remain to be elucidated. The great majority of the hairs are in some way feathered or toothed, and the lateral members which they then bear may be of every relative dimension and shape, from the finest filaments to the coarsest serration, may vary in different parts of the same hair, be directed at any angle to the axes, or recurved, as on some of the hairs of the epipodites, and be set on one side of it, on two, or on all sides. Most of the hairs are placed on edges or surfaces where they meet the water, either actively in the movement of the limb or passively by the flow of the gill-stream. From their form and position it is clear that they must serve more uses than one, though whether any of them have a double function is less obvious. Some of them undoubtedly serve to *filter* the water entering various orifices. This is clear from the particles with which they may often be seen to be laden. It is notably the function of those which outline the parts of the operculum formed by the third maxilliped, and on its coxa help to guard the opening of Milne-Edwards, as all the openings of the gill-chamber are guarded by hairs on the carapace and on the coxæ of the legs.

Others are *sensory*. Most if not all of these are probably tactile, that is give information as to the pressure which is exerted against them, but their sensibility is used in various ways. It is clear from its behaviour that the crab is able to detect the presence of particles in any part of its gill-stream and accordingly to stop, reverse, or alter its direction. This can only be due to tactile organs at various points in the system. Another use of the tactile sense is involved in the appreciation of the strength of the current, which the animal must possess. Conceivably this might be due to a muscular sense of the power used in producing the current, but, as Doflein (6) has shown, it is very probable that in Crustacea the muscular sense is supplemented, if not largely replaced, by the information given by tactile hairs brought against the water by the movement of the limbs. In any case, it is likely that this information is possessed by the crab and guides it in the use of its limbs. Probably the more delicately feathered hairs are those which are exposed to and detect finer changes in the pressure of the water. From these there is a gradation to the coarser ones which are used in filtering. Whether any or all of the latter are sensitive does not appear.

Whether, again, any of the pairs subserve a chemical sense is doubtful. Certainly the behaviour of the crab shows that it possesses such a sense, and by it is informed of the quality of the water and of the nature of the food. But it is quite possible that this is due to the antennules. Over these the water passes on leaving the gill-chamber, and the juices and débris of the food are rejected towards them, and probably to some extent reach them in spite of or by permission of the exopodites of the maxillipeds. The crab appears, though less clearly than a prawn, to taste as well as to smell its food, but this may be due to the sensibility of the antennule; much as in Man, the aromas of food are appreciated by the olfactory epithelium.

Others of the hairs have a *cleaning* function. This is exercised in very different ways by the long threads on the epipodites of the maxillipeds (and possibly by the coxopoditic setæ of the maxillule, for which I can suggest no other function), and by the serrated bristles of the palps of the third maxillipeds. Those organs are continually busy cleaning the various structures in front of them. They brush the antennules, sometimes acting singly, sometimes combing an antennule between them. Each of them brushes the eye and antenna of its side, and reaches across to clean the mouth-parts of the opposite side, attending, for instance, to the delicate and probably sensory hairs of the expanded end of the endopodite of the first maxilliped. In these activities, different parts of the palp are brought each against a different organ, and very possibly the difference in the serration of the bristles in various parts is in correspondence with the structures to be cleaned in the organs to which they are applied.

The function of *current-making* must perhaps be attributed to the hairs on the flagella of the exopodites.

Lastly, the bristles which are used in *manipulating the food* are special members of the series of hairs.

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EXPLANATION OF THE PLATES.

Plate 10.

Fig. 1. A ventral view of a female of the Shore Crab (*Carcinus mænas*). On the left side of the animal the first and second walking-legs have been parted, to expose the approach to the inhalent opening between them, and on the right side the cheliped has been turned back to reveal as much as possible of the flange on the coxa of the third maxilliped, by which the inhalent opening of Milne-Edwards is guarded.

Fig. 2. The forepart of a similar view after the third maxillipeds have been divaricated, one of them cut short beyond its basis, and the chelipeds removed with the exception of their coxæ.

Fig. 3. A ventral (posterior) view of the third maxilliped of the right side, removed from the body and flattened. The dotted lines show the normal position of the epipodite. The small drawing annexed shows a portion of the dorsal (anterior) surface of the ischium of the yellow appendage, enlarged.

Fig. 4. A similar view of the second maxilliped of the right side.

Fig. 5. A similar view of the first maxilliped of the right side.

Fig. 6. A similar view of the maxilla (second maxilla) of the right side.

Fig. 7. A similar view of the maxillule (first maxilla) of the right side.

Fig. 8. A similar view of the mandible of the right side.

Fig. 9. A view of the mouth and of the structures around it, after removal of all the paired appendages save the maxillule and mandible of the right side.

Fig. 10. A diagram of a transverse section through the branchiostegite and the structures which underlie it at the level of the articulation of the first walking-leg.

Fig. 11. A diagram of a longitudinal section through the branchial chamber of the left side. The podobranch of the second maxilliped is shown in perspective, and the position of the arthrobranchs of the third maxillipeds is indicated in dotted lines.

Fig. 12. A view of the Crab from the left side after removal of the branchiostegite. Part of the inner roof of the gill-chamber remains, and is held back by a hook above the third walking-leg.

Fig. 13. A view from within of a portion of the removed branchiostegite of the same side.

Fig. 14. A view from below of the inhalent openings above the first and second walking-legs of the same side.

Fig. 15. A view from above of the gill-chamber of the same side. The portions of the inner roof which have not been removed are held back by hooks.

Fig. 19. Portions of hairs from the third maxilliped:—A, from the median band of the ischium; B, from the palp of the same limb; C, from the flagellum of the exopodite.

Plate 11.

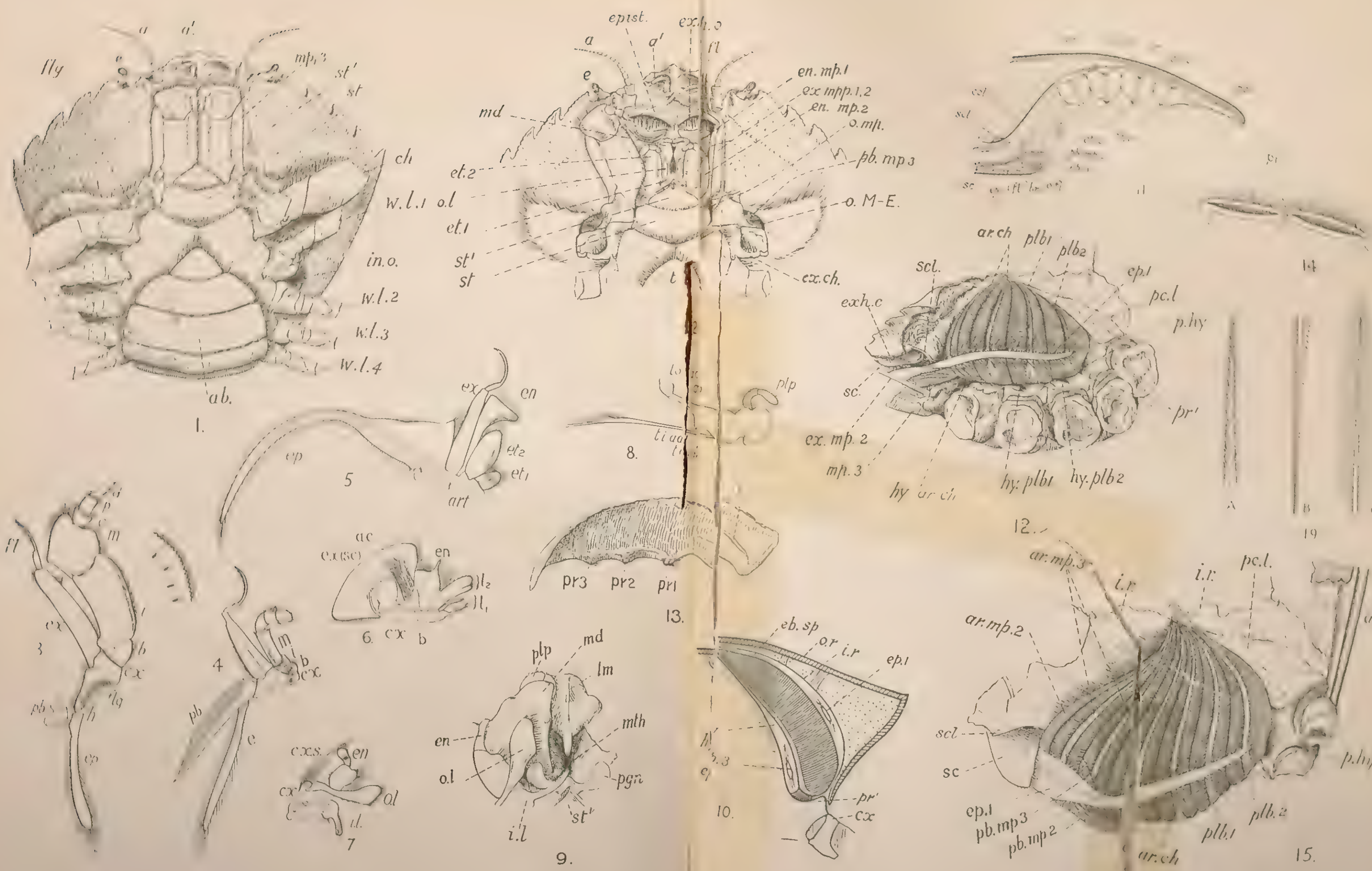
Fig. 16. A view similar to that in Fig. 15, after the removal of the greater part of the gills.

Fig. 17. A similar view after complete removal of all the gills, save those of the second maxilliped, the third maxilliped being in the normal position.

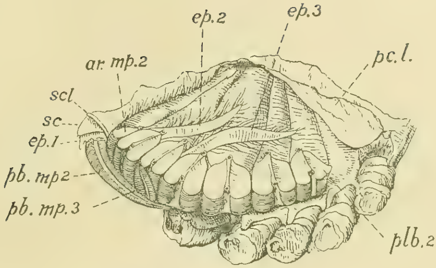
Fig. 18. A similar view with the third maxilliped divaricated from its fellow.

Explanation of the lettering of the figures.

a. antenna.
a'. antennule.
ab. abdomen.
ac. accessory muscles.
ap. apophysis.
ar.ch. arthrobranchs of cheliped, or stumps of same.
ar.mp. (*2, 3*). arthrobranchs of maxillipeds.
art. articulation.
b. basis.
br. branchial ridge.
c. carpus.
ch. cheliped.
col. collecting space.
cx. coxa.
cx.s. coxopoditic setæ.
d. dactylus.
e. eye.
eb.c. epibranchial channel.
eb.sp. epibranchial space.
en. endopodites.
en.mp. (*1, 2*). endopodites of maxillipeds.
ep.(*1,2,3*). epipodites.
epist. epistome.
et. (*1, 2*). endites of first maxilla.
ex. exopodite.
ex.mp. (*1, 2*). exopodites of maxillipeds.
exh. c. exhalent canal or passage.
exh. o. exhalent opening.
fl. flagella.
flg. flange.
h. hinge.
hy. hypobranchial space.
hy. ar. ch., *hy. plb.* (*1, 2*). openings in front of gills, leading to hypobranchial space.
i. ischium.
i. fl. inner floor.
i.l. inner lacinia.
i.r. inner roof.
in.o. approach to inhalent opening.
l. (*1, 2*). cleft lobes of maxilla.
lm. labrum.
m. merus.
md. mandible.
mp. (*1, 2, 3*). maxillipeds.
mth. mouth.
o.l. outer lacinia.
o.fl. outer floor.
o.r. outer roof.
o.mp. opening leading to gill-chamber, in front of third maxilliped.
o.M.E. opening of Milne-Edwards.
p. propus.
p.hy. posterior opening of hypobranchial chamber.
pb. (*1, 2*). podobranchs.
pc.l. pericardial lobe.
pgn. paragnathum.
plb. (*1, 2*). pleurobranchs.
plp. palp of mandible.
pr. (*1,2,3*). processes upon rim of branchiostegite which meet corresponding processes above articulations of legs.
pr'. processes above articulation of legs.
sc. scaphognathite.
scl. sclerite.
st. sternum of third maxilliped.
st'. fused sterna of mouth-parts in front of third maxillipeds.
t.i.ad. tendon of inner adductor.
t.o.ab. tendon of outer abductor.
t.o.ad. tendon of outer adductor.
w.l. (*1, 2, 3, 4*). walking-legs.



MOUTHPARTS OF SHORE CRAB



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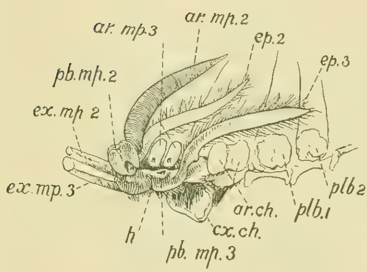

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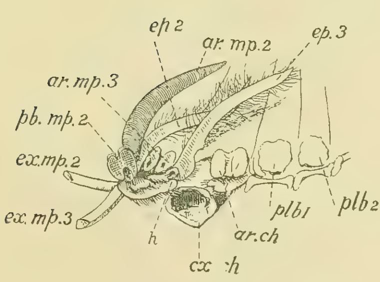

3.

MOUTHPARTS F SHORE CRAB

Grout, photo. sc. & imp.